# HETEROCHRONIC TRENDS IN NAMURIAN AMMONOID EVOLUTION

## *by* ANDREW R. H. SWAN

ABSTRACT. Theoretical models of heterochronic processes are based on the comparison of ontogenetic age-shape curves of ancestor and descendant. An existing principal components analysis of an exhaustive body of Namurian ammonoid morphological data is a suitable source of information for assessment of heterochrony in this context. Using size as an indicator of age and principal component score as a shape index, heterochronic analyses of two evolutionary radiations of the Gastriocerataceae demonstrate that one was strongly influenced by neoteny, the other by acceleration. From an ancestor which undertook a change in habitat during ontogeny from benthic to nektonic, the occupation of the benthic habitat was increased in the neotenous trend and decreased in the lineage showing acceleration. Widespread changes in marine benthic conditions are suggested as the cause of these trends.

THIS paper compares the ontogeny with the evolutionary trends of Namurian (mid-Carboniferous) ammonoids in order to evaluate the contribution of heterochronic processes. There is a long history of ammonoid studies of this sort, due largely to the good record of ontogeny exhibited by many specimens. Ammonites were cited as evidence of recapitulation by, for example, Hyatt (1889), and of proterogenesis by Schindewolf (1936). Carboniferous ammonoids do not have such a history of analysis in this context, although Newell (1949) documented phyletic size increase in an Upper Palaeozoic ammonoid lineage which included Pennsylvanian forms. The restriction of the present study to Namurian ammonoids is due to the existence of an extensive and appropriate data base with accompanying analyses compiled by Saunders and Swan (1984).

Heterochrony has been defined by Gould (1977) after de Beer (1930) as: 'phyletic change in the onset or timing of development, so that appearance or rate of development of a feature in a descendant ontogeny is either accelerated or retarded relative to the appearance or rate of development of the same feature in an ancestor's ontogeny.' Following the publications of Alberch *et al.* (1979) and McNamara (1986), the terminology of heterochronic processes has been clarified (text-fig. 1). Where the mature morphology of a descendant is similar to the immature morphology of its ancestor, the result is termed paedomorphic; where the opposite is true, the descendant is peramorphic. A paedomorphic descendant can arise by a decrease in the rate of change of morphology in ontogeny (neoteny), by early attainment of maturity (progenesis), or by delayed onset of morphological change. Paedomorphosis results in the loss of some morphologies from the ontogeny. Peramorphosis occurs by increase in the rate of change of morphology (acceleration), by late maturity (hypermorphosis) or by early onset of morphological change, and involves transcendance into morphologies absent from the ancestral ontogeny.

In this terminology, recapitulation results from peramorphosis and phyletic size increase may be due to hypermorphosis. Proterogenesis, however, is not a purely heterochronic process, but requires a morphological innovation specifically in early ontogeny: an event known as cenogenesis. This novelty then spreads to the adult stage, perhaps by neoteny (text-fig. 2).

The evolutionary importance of the heterochronic processes results from the potential of achieving great changes in mature morphology by isolated mutations in the regulatory genes. Through such mutations, major morphological changes are not accompanied by the high risk of low viability which is invoked by large-scale structural mutations resulting in 'hopeful monsters'. In the case of paedomorphosis, the viability of the resulting adult is likely to be high, due to the previous viability of the same morphology in the juvenile. In addition to his arguments for the

**PAEDOMORPHOSIS**



**PERAMORPHOSIS**
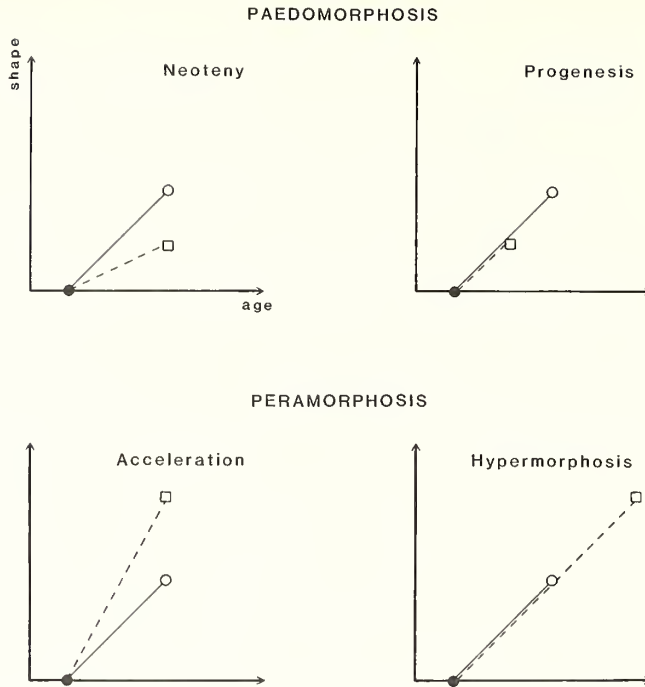


TEXT-FIG. 1. Definitions of heterochronic modes on the basis of ontogenetic trajectories of ancestor (solid line) and descendant (dashed line). The onset of morphological change is indicated by a solid circle; cessation is indicated by an open circle for the ancestor, a square for the descendant.

In paedomorphosis, the terminal shape of the descendant is the same as the shape of a younger ancestor; in peramorphosis, the terminal shape of the ancestor is the same as the shape of a younger descendant. In neoteny and acceleration there is change in the ontogenetic gradient; in progenesis and hypermorphosis there is change in the length of time during which shape change occurs.

Redrawn from Alberch et al. (1979, figs. 15 and 16).

evolutionary importance of heterochrony, Gould (1977) contended that certain heterochronic modes are compatible with specific ecological strategies: progenesis with r-type strategy (rapid reproduction allowing opportunistic colonization), and neoteny with K-strategy ('fine tuning' to a stable environment with high investment in few offspring).

Analysis of heterochrony in Namurian ammonoid evolution is therefore significant both in the continuing global assessment of modes of evolution and in the interpretation of specific Namurian evolutionary trends and environments. The recently rationalized terminology of heterochrony has given the procedure of heterochronic analysis a well-defined suite of requisites and criteria which form the basis of the methodology in this study.

## DATA USED

The approach used here is strongly dependent on the principal components analysis of an extensive data base presented by Saunders and Swan (1984). These data include measurements of size and external morphology (expressed by 20 shape variables which incorporate shell geometry, aperture form and ornament, see Table 1) of 371 Namurian ammonoid specimens (281 species, 81 genera), compiled largely from published illustrations. An attempt was made to include all published species from North-West Europe, the South Urals (USSR), and North America, though many species

TEXT-FIG. 2. Theoretical sequence of ontogenetic trajectories resulting in proterogenesis. The first descendant (2) of the ancestor (1) differs from it due to an evolutionary innovation affecting only early ontogeny (cenogenesis). This innovation then spreads to later ontogeny in subsequent descendants (increments 3 to 5) by neotenous decrease of ontogenetic gradient.
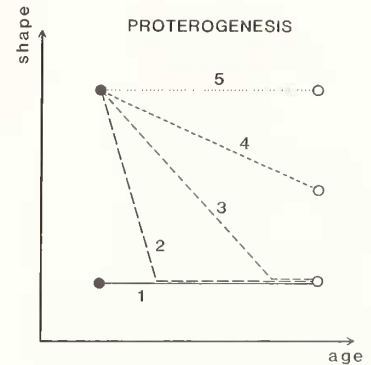


TABLE 1. Representative values of characters for the Namurian ammonoid morphotypes relevant here, with the contribution of each character to the first three principal components of variation.

Character abbreviations: D, diameter of umbilicus; AH, aperture height; S, whorl shape; VW, ventral acuity; W, whorl expansion rate; OW, areal expansion rate; T, spacing of transverse ornament; TVS, spiral *versus* transverse ornament; LT, plication or tubercle length; HT, plication or tubercle elevation; RIB, ribbing strength; ARC, arching of aperture; HS, depth of hyponomic sinus; OS, depth of ocular sinus; UP, umbilical aperture projection; VG, ventral structure; VLG, ventrolateral structure; UR, umbilical ridge; CON, number of constrictions; BIF rib bifurcation.

Most of these are expressed as ratios; see Saunders and Swan (1984) for definitions and additional details of each character.

| Character | Morphotype | | | | P.C. loadings | | |
|-----------|---------|--------|--------|--------|---------|---------|---------|
|           | III     | V      | VII    | VIII   | P.C.1   | P.C.2   | P.C.3   |
| D    | 0·307 | 0·133  | 0·433 | 0·45  | 0·885  | 0·069  | −0·017 |
| AH   | 0·586 | 0·55   | 0·565 | 0·624 | 0·237  | 0·502  | 0·373  |
| S    | 1·49  | 1·2    | 1·75  | 1·58  | 0·757  | −0·257 | −0·236 |
| VW   | 0·476 | 0·437  | 0·446 | 0·527 | −0·102 | 0·083  | −0·05  |
| W    | 2·12  | 2·18   | 1·51  | 1·62  | −0·529 | 0·295  | 0·328  |
| OW   | 0·77  | 1·18   | 0·611 | 0·595 | −0·785 | 0·254  | 0·153  |
| T    | 10·0  | 6·0    | 16·0  | 18·0  | −0·226 | 0·274  | −0·553 |
| TVS  | 0·8   | 1·0    | 1·0   | 0·8   | 0·026  | −0·154 | 0·423  |
| LT   | 0·3   | 0·0    | 0·0   | 0·65  | 0·659  | 0·521  | 0·093  |
| HT   | 0·025 | 0·0    | 0·0   | 0·02  | 0·65   | 0·411  | 0·158  |
| RIB  | 0·2   | 0·9    | 0·0   | 0·2   | 0·304  | −0·134 | 0·734  |
| ARC  | 9·0   | −12·3  | −0·7  | 13·0  | 0·683  | 0·193  | −0·239 |
| HS   | 21·0  | 10·1   | 1·7   | 3·5   | −0·555 | 0·618  | 0·074  |
| OS   | 24·5  | 0·5    | 0·0   | 11·0  | 0·099  | 0·807  | −0·194 |
| UP   | 0·0   | 1·5    | 2·0   | 0·0   | −0·579 | 0·067  | 0·109  |
| VG   | 1·1   | 1·0    | 1·0   | 1·0   | −0·283 | −0·067 | 0·107  |
| VLG  | 0·8   | 1·0    | 1·0   | 1·0   | 0·094  | −0·554 | 0·174  |
| UR   | 0·0   | 0·0    | 0·0   | 0·0   | −0·005 | −0·149 | 0·041  |
| CON  | 3·0   | 0·0    | 0·0   | 3·0   | 0·31   | 0·047  | −0·281 |
| BIF  | 1·0   | 2·0    | 1·0   | 3·0   | 0·507  | 0·125  | 0·553  |
|      |       |        |       | Total % | 24·4 | 12·32  | 9·08   |

had to be eliminated from analysis due to incomplete morphological data. Other faunas, for example from North Africa and China, are at present only partially documented. For each specimen the general location and stratigraphic level were recorded. The data were originally compiled with the objective of including the whole range of morphologies present, regardless of size. Consequently, where possible, species were assessed at two different sizes (10-25 mm and > 25 mm) to allow for ontogenetic change, though the exact sizes used were dictated by the available documentation. Specimens smaller than 10 mm diameter were not assessed due to paucity of information and difficulty of measurement.

Within the realms of logistical feasibility, it would be difficult to improve on this data base as a source of information on Namurian ammonoid morphology with respect to ontogeny, time, and space. The data have been deposited with the British Library, Boston Spa, Yorkshire, UK, as supplementary publication no. SUP 14032 (41 pages).

## TAXA CONSIDERED

Saunders and Swan (1984, figs. 13-20) documented the changes in the diversity of external morphology of ammonoids through the Namurian of North-West Europe, North America, and the South Urals. Some taxa were shown to be morphologically conservative (e.g. Dimorphocerataceae, Prolecanitina) while others declined (e.g. Neoglyphiocerataceae) or became extinct (e.g. Muensterocerataceae). The Gastriocerataceae, in contrast, arose within the Namurian and evolved rapidly, showing radiation and innovation into new morphologies. The most striking trends in the evolution of this superfamily were the development of two distinctive morphotypes: 1, evolute, depressed, coarsely ornamented forms with fairly simple apertures, e.g. *Cancelloceras*; 2, involute, compressed forms with strong hyponomic and ocular sinuses and prominent ventrolateral lingua, e.g. *Bilinguites*. In Saunders and Swan's (1984) principal components analysis of twenty external morphologic characters in 281 Namurian ammonoid species, these two morphologies are resolved as positive P.C.1, low P.C.2 scores (designated morphotype VIII), and as positive P.C.2, low P.C.1 scores (designated morphotype III), respectively (text-fig. 3; Table 1). The development of these two morphotypes in the Gastriocerataceae is the focus of the heterochronic analysis in this paper. The constituent families of the Gastriocerataceae are: Homoceratidae, Decoritidae, Reticuloceratidae, Gastrioceratidae, and Bisatoceratidae.

## CONSTRAINTS ON THE DATA

Unambiguous recognition of heterochrony according to the scheme of Alberch *et al.* (1979) requires the following: 1, knowledge of ancestor-descendant relationship; 2, recognition of ontogenetic stages corresponding to the onset and cessation of morphologic change; 3, age at these stages; 4, shape at these stages; and 5, size at these stages (only needed to resolve the special cases of proportioned gigantism and dwarfism). The problems associated with satisfying each requisite for the chosen group of Namurian ammonoids must be carefully considered.

*Ancestor-descendant relationship*

The Namurian marine record is punctuated by strong eustatic regressive events in all the important stratigraphic sections (Ramsbottom 1977; Saunders *et al.* 1979); consequently it is not possible to trace individual lineages through the succession with any confidence. This limits the analysis to trends, rather than details, in evolution. Hence the comparison is of successive faunas rather than species, and only fairly major morphological shifts can be resolved. For this situation, the methodology only demands that the stem groups of the analysed species in each fauna are included within the data for the chronologically previous fauna. The more recent of the relevant phyletic hypotheses are generally supportive (Ruzhencev and Bogoslovskaya 1978; Swan 1984); specific problems will be assessed where appropriate. It should be noted that faunas from North-West Europe, the South Urals, and North America (the main sources of data) are not phyletically
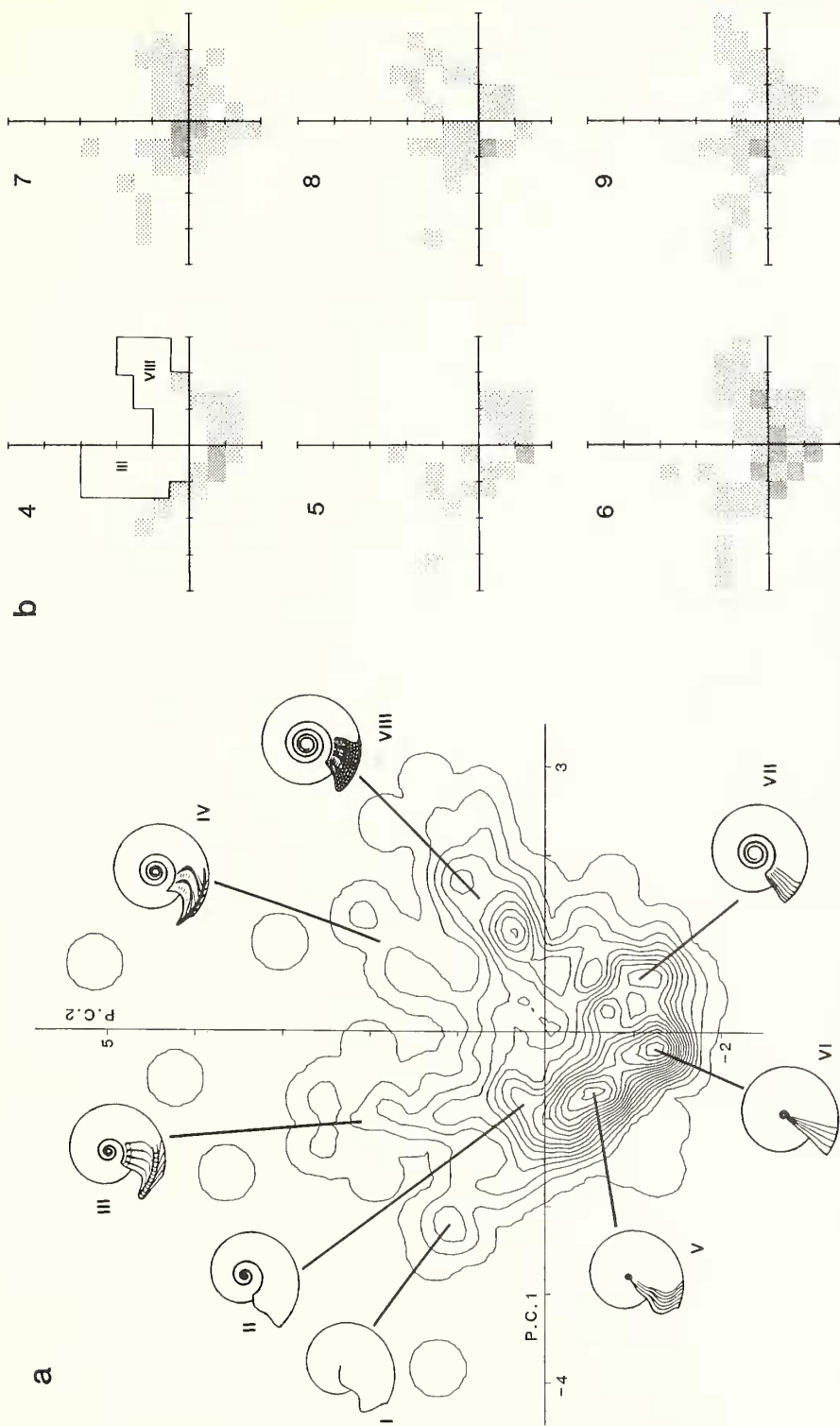
TEXT-FIG. 3. a, density contours for the distribution of Namurian ammonoids in the first two principal components of variation, based on the analysis of Saunders and Swan (1984). Representatives of the eight morphotypes are illustrated and their approximate positions on the plot are given. (From Swan and Saunders 1987, fig. 1.) b, the distributions of Namurian ammonoids with respect to the same principal components through six increments of time (levels 4–9 of Saunders and Swan 1984) from H zone to G zone. 1/2 P.C. squares are stippled if they include at least one specimen; heavier stippling indicates > 4 specimens. The enclosed areas indicated on the level 4 diagram show the limits of morphotypes III and VIII, as defined for the purposes of the present study.

discrete; they share many genera and some species throughout the Namurian, due presumably to migration during transgressive maxima. This validates the analysis of the disparate regions together.

*Ontogenetic stages*

The onset of morphological change can readily be regarded in ammonoids as the earliest secreted structure—the protoconch. The cessation of morphological change is also definable in ammonoids because, like recent *Nautilus* (Saunders 1983) there is decline and cessation of growth at maturity. Recognized symptoms are: approximation of septa, development of apertural modifications, change in aperture size or shape (for example by constriction), decline in ornament, and change in tightness of coiling (Kennedy and Cobban 1976). The recognition of cessation of morphological change is critical in documenting progenesis and hypermorphosis because, for example, a hypermorphic descendant identical to the terminal morphology of its ancestor only differs from it in that its ontogeny continues.

However, problems exist in the consistent identification of maturity in Namurian ammonoids. Documentation of symptoms of maturity is not as thorough as for Mesozoic forms, so the application of criteria is open to doubt. Septa are not readily observable in most specimens, ornament frequently declines long before maturity, changes in coiling are never more than subtle, apertures do not show the extreme modifications associated with sexual dimorphism in the Mesozoic, and in any case they are often destroyed by various taphonomic processes along with the rest of the body-chamber. Detailed knowledge of the terminal stage of ontogeny is therefore unavailable for most Namurian species. In addition, the use of symptoms of maturity in these analyses may be inadvisable in that they may be intimately linked with gonadal development. Hence the apertural modifications associated with sexual maturity of an ancestor may be expected to occur at maturity in a neotenous descendant, even though up to that point the descendant morphology had been that of the juvenile ancestor.

At the expense of precision, size is here adopted as an indicator of ontogenetic stage, as it is the only remaining parameter which is at all correlatable with development. The effect of this imprecision on the results is discussed later.

*Age*

Age provides the measure of ontogeny used on the *x*-axis of the theoretical ontogenetic trajectories of Alberch *et al.* (1979) (text-fig. 1). It is, of course, notoriously difficult to assess in fossil material. Estimates for age at maturity of ammonoids are all contestable and vary from 4 to 30 years; it is clearly not feasible to ordinate large numbers of specimens against an age axis. Once again, size is the only available parameter conceivably related to age. The tentative equation of size and age precludes the recognition of proportioned gigantism and dwarfism, and renders the result of heterochronic analysis indefinite to a degree which will be discussed later.

*Shape*

The theoretical ontogenetic trajectories established for heterochronic analysis (text-fig. 1) use a single parameter on the *y*-axis to characterize shape. Although various authors have used univariate data to discern heterochrony (e.g. Newell 1949), this procedure is logically unsound. If an ancestral ontogeny involves the change in a single character value from p to q, then a mature value in the descendant of between p and q could be regarded as due to a type of paedomorphosis; a value beyond q could be regarded as due to peramorphosis, even though the change might be the result of any evolutionary mode. Therefore, in some cases, any conceivable character value in the mature descendant could be explained by a heterochronic process and the hypothesis of heterochrony would not be falsifiable.

With reference to the theoretical age–shape trajectories (text-fig. 1), this situation can be stated in terms of vectors. The various heterochronic modes are transformations of the ancestral ontogeny which, in combination, could produce any result in the plane defined by the age and shape axes,

providing the direction ($+$ or $-$) of the gradient is conserved. However, the test of the heterochronic hypothesis improves if more characters are used, increasing the dimensionality of shape–space. As a result, the descendant ontogenetic trajectory is not constrained within the plane defined by the age axis and the ancestral trajectory. If the descendant trajectory *is* within this plane, then a heterochronic hypothesis is supportable, and becomes more so with larger numbers of dimensions of shape–space. Heterochronic studies should therefore consider as many morphological characters as possible.

Whole morphology has been assessed in heterochronic studies by many authors (e.g. McNamara 1982) but rarely with any numerical reinforcement. Gould (1968), however, used factor analysis of seven shape measurements to demonstrate the similarity between adult snail paedomorphs and juvenile non-paedomorphs on a plot with two varimax axes. The eigenvectors which form the basis of this type of multivariate analysis are directions in multi-dimensional shape–space; consequently, if a plane defined by an eigenvector and the age axis contains both ancestral and descendant ontogenetic trajectories, then heterochrony is a likely hypothesis. Eigenvectors are therefore an appropriate means of resolving shape as one parameter which can be used for constructing ontogenetic trajectories for comparison with the theoretical heterochronic modes of Alberch *et al.* (1979).

In this context, the principal components analysis of Saunders and Swan (1984) is a suitable source of data. Much of the information contained in the 20-character data set for each specimen is conveyed by co-ordinates in three-dimensional principal component (= eigenvector) space. Although one principal component describes no more than 25 % of the total variation, the two evolutionary radiations chosen for the present work, namely the gastrioceratacean excursions into morphotypes III and VIII, are roughly linear in at least the first two principal components. The score against one of the principal component axes for these morphotypes consequently gives a good estimate of total morphology. For morphotype VIII, the score on the P.C.1 axis is appropriate; for morphotype III, the score on the P.C.2 axis.

*Size*

Size is the least problematic of the required parameters. Diameter of the conch is a standard measure of ammonoids, and is adopted here. The possible objection that this does not necessarily correlate with body volume is not critical because body-chamber length is fairly consistent within the Gastriocerataceae, and whorl height tends to be inversely correlated with whorl width, giving little variety in whorl cross-sectional area (Swan and Saunders, 1987). For each species, Saunders and Swan (1984) assessed morphology in two different size ranges: at 10–25 mm diameter and > 25 mm diameter, wherever possible. The lack of data on smaller sizes was imposed by the available published information, and there is seldom any definite knowledge of the maximum size attained by species, which is likely to be in excess of the largest documented specimen. Consequently, the data available from this study are of segments of ontogeny of variable length, usually without knowledge of morphology at onset or cessation of growth.

In summary, the information available is in some respects not ideal for the stringent assessment of heterochrony; it corresponds to the third restricted model of Gould (1977, p. 260): standardization by size when neither age nor developmental stage are known. Nevertheless, as noted by Gould, it is typical of the quality of data available to palaeontologists. It is likely that most palaeontological heterochronic analyses will have to proceed using some of the assumptions adopted here, and care must be taken to interpret the results with due consideration to the assumptions, and to use the results to review their validity.

## ARRANGEMENT OF THE DATA AND GRAPHICAL ANALYSIS

Ontogenetic trajectories, expressed as curves of shape (principal component score) against size (diameter) are required for potential ancestors and descendants amongst the Namurian

Gastriocerataceae which adopted morphotypes VIII and III. Data are selected and arranged as follows:

*Morphotype VIII*

The radiation into this morphotype occurred apparently abruptly at level 6 of Saunders and Swan (1984) (text-fig. 3*b*). However, distinct stratigraphic horizons within level 6, though not confidently correlatable between continents, are recognized locally and can be used to improve the resolution. For this purpose the stratigraphic detail used here is at the zonal level; zones used are: in North-West Europe, $H_{2c}$, $R_{1a1}$, $R_{1a2}$, $R_{1b}$, $R_{1c}$, $R_{2a}$, $R_{2b}$, $R_{2c}$, $G_{1a}$, $G_{1b}$; in the USSR, $Nm_2b_1$, $Nm_2b_2$, $Nm_2b_3$, $Nm_2c_1$, $Nm_2c_2$. Data for this morphotype from North America are sparse (five specimens) and are not considered here due to problems in correlation. The isolated incursion into morphotype VIII in level 4 (text-fig. 3*b*) is ignored as this species, *Homoceras alveatum* Ruzhencev and Bogoslovskaya (1978), is only known from one apparently pathological specimen. With these exceptions, the complete data for all specimens recorded by Saunders and Swan (1984) in each of the zones listed above which have at least part of their ontogeny in morphotype VIII (as defined on text-fig. 3*b*) have been plotted. The result is shown in text-fig. 4, and representative morphologies are illustrated in text-fig. 5.

*Morphotype III*

The adoption of this morphology by the Gastriocerataceae was not abrupt, but shows increasing strength through zones $R_{1a}$ to $R_{2c}$ ($Nm_2b_2$–$Nm_2c_2$ in USSR). For this reason, and the lesser quantity of information available, the stratigraphic resolution into the four levels 6–9 of Saunders and Swan (1984) provides adequate account of the evolution of this morphology. Note that, although this study only concerns the Gastriocerataceae, morphotype III was extensively represented by girtyoceratids earlier in the Namurian (which declined in level 3, $E_{2c}$ zone), and by the conservative and rare nomismoceratids, *Hudsonoceras* and *Baschkirites*, in the later Namurian (levels 5–9, zone $H_{2a}$ onwards). The gastrioceratacean genus *Bilinguites* is to an extent homoeomorphic with these genera.

As with morphotype VIII, the complete data for all Gastriocerataceae in each of the stratigraphic levels which have at least part of their ontogeny in morphotype III (as defined in text-fig. 3*b*) have been plotted. The result is shown in text-fig. 6, with representative morphologies illustrated in text-fig. 7.

INTERPRETATION OF RESULTS

*Morphotype VIII*

Two important features are apparent on examination of the graphical results (text-figs. 4 and 5) and the interpretative, schematic summary (text-fig. 8*a*). First, the innovation into this morphotype initially occurs only in the smaller ontogenetic stages: in level 6 there are no specimens larger than 30 mm diameter in this quadrant of the principal components plot, and the ontogenetic gradients are steep. The innovation of this morphotype, therefore, can be described as cenogenesis, and this is not a heterochronic process. Secondly, whilst the morphology at small sizes is retained or accentuated, the ontogenetic gradients decline through time (text-fig. 9), with the result that later stages in ontogeny become more similar to the early stages, and similarity tends to be between early ontogeny of ancestors and late ontogeny of descendants. If these graphs are compared directly with the theoretical models (text-fig. 1), it is clear that this decline in ontogenetic gradient is compatible with neoteny.

Before the hypothesis of neoteny is confirmed, the effect of the assumptions needs to be discussed. The assumption of descent between successive faunas is not in question for much of the data; for example, Ruzhencev and Bogoslovskaya (1978, pp. 59–60) and Swan (1984, p. 319) both traced a simple lineage through the morphotype VIII reticuloceratids (levels 6–7). However, the relationships with higher and lower faunas are uncertain. The earliest European species in the present analysis
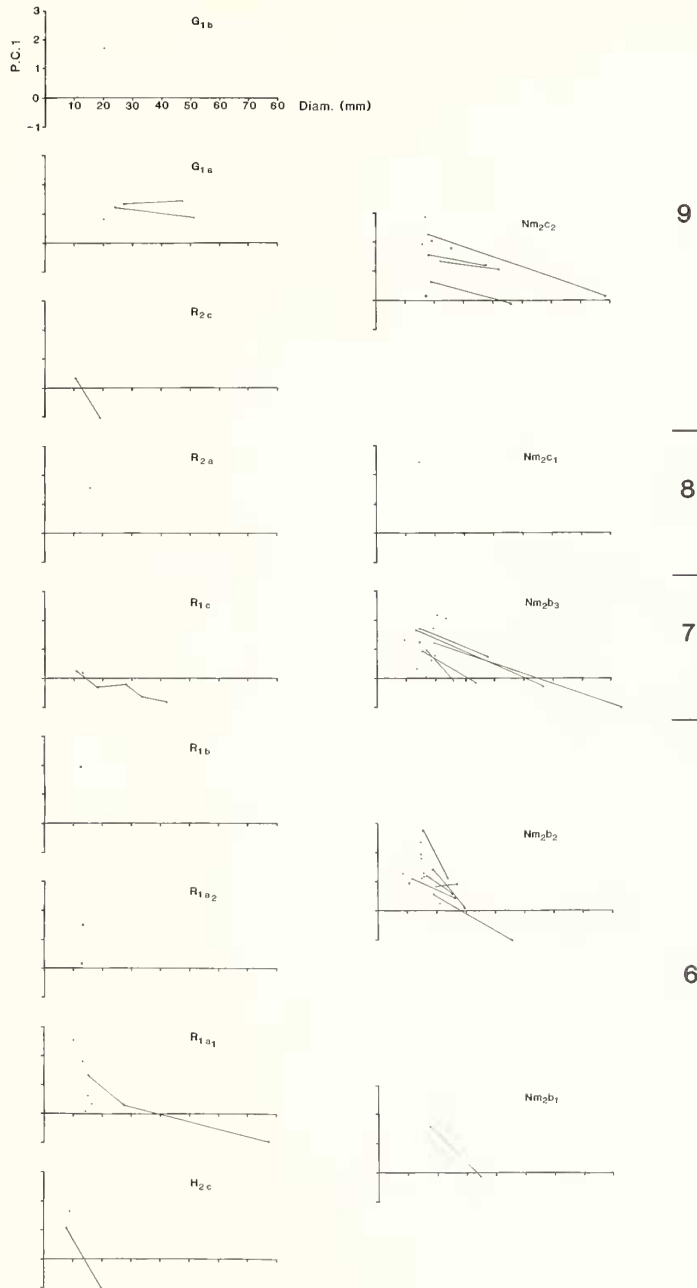
TEXT-FIG. 4. Size *versus* first principal component score for all analysed species with at least part of ontogeny in morphotype VIII. Data points from the same species are connected by lines.

The data for each zone are plotted separately; zonal schemes of North-West Europe (*left*) and southern Urals (*right*) are approximately correlated and in stratigraphic order (youngest at top) with the stratigraphic levels (6-9) of Saunders and Swan (1984) indicated on the far right; international correlation within each level is not definite. Labelling on all axes as for $G_{1b}$ zone.

The graphs show a general evolutionary decline in ontogenetic gradient. The faunas from zones $R_{1c}$, $R_{2a}$, and $R_{2c}$ are not part of the main morphotype VIII phylogenetic lineage.
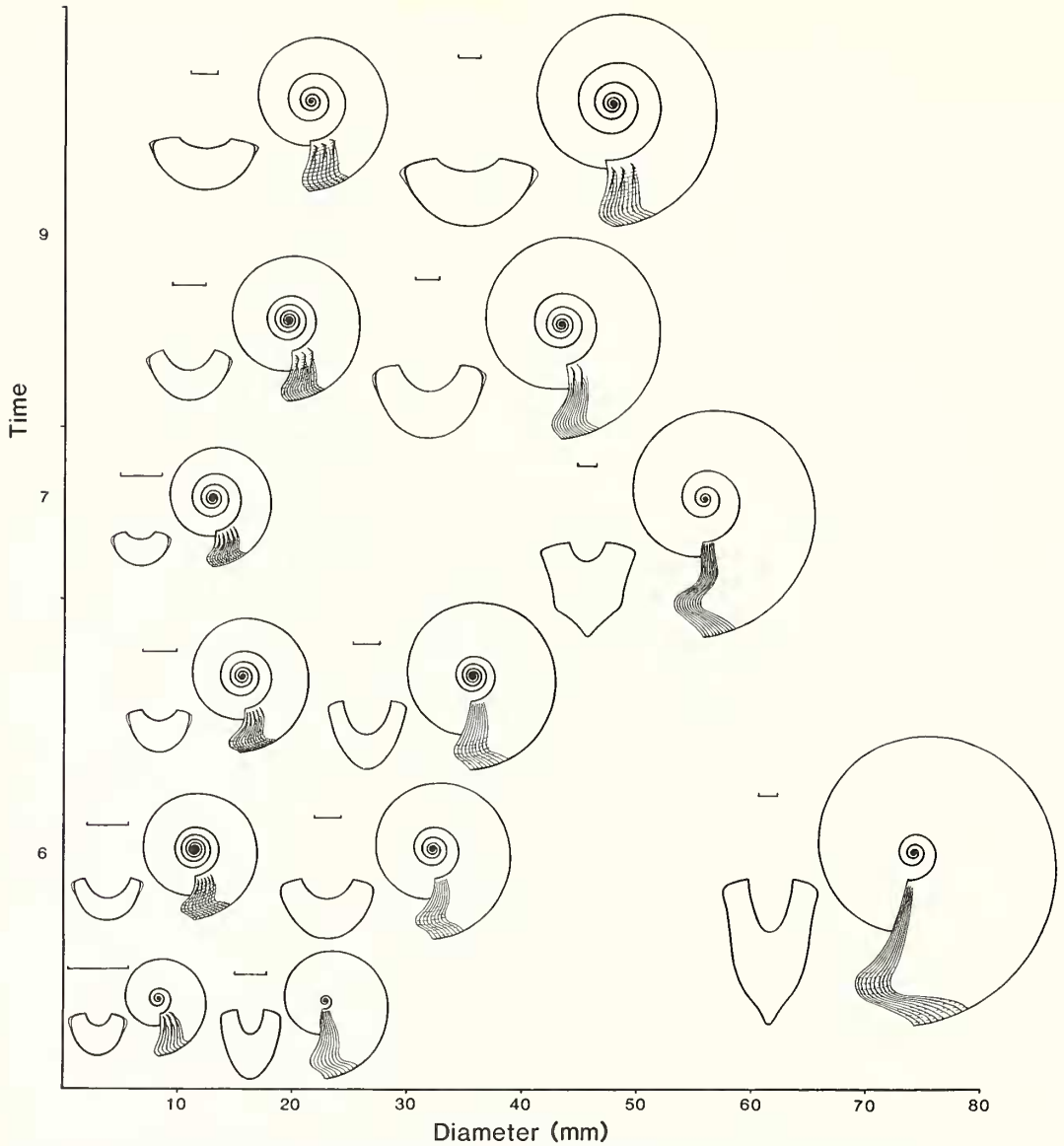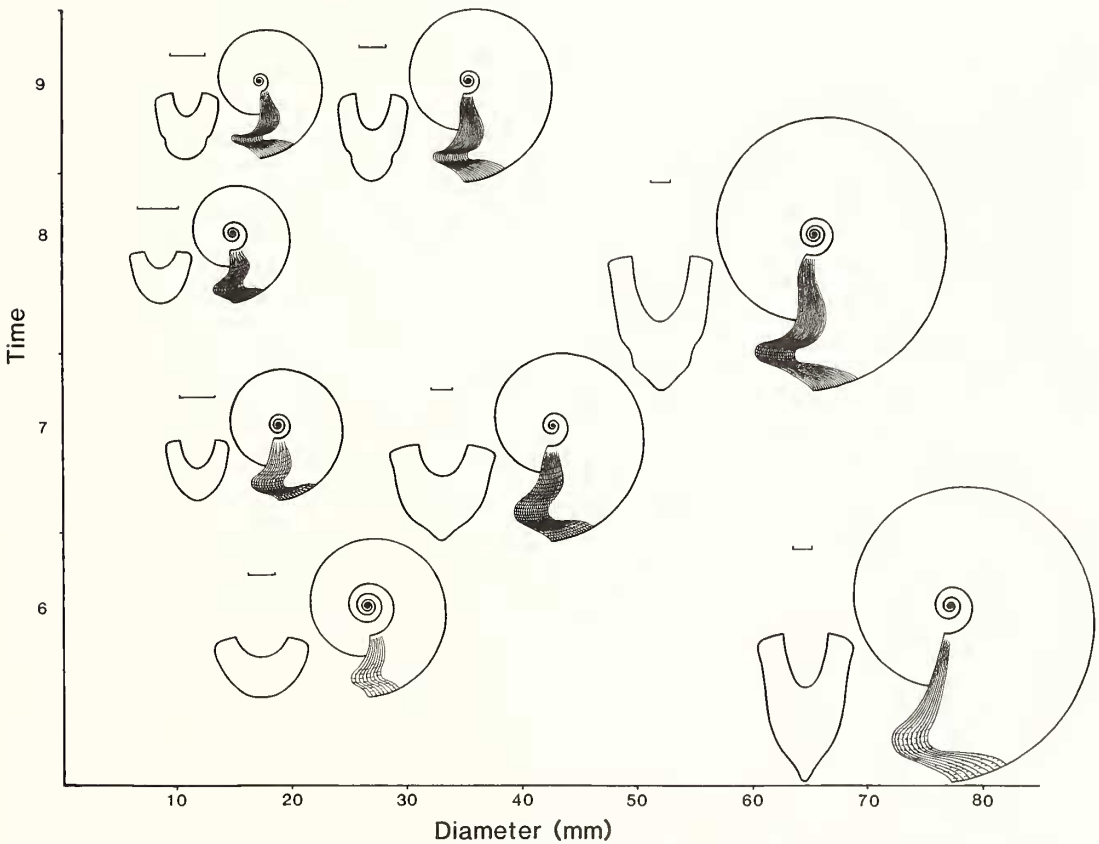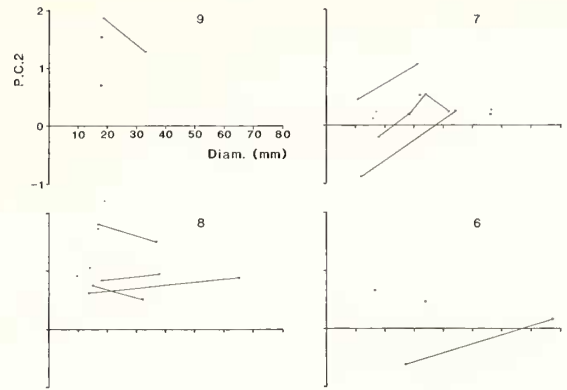
TEXT-FIG. 5. The development of morphotype VIII, illustrated by sketch profiles (with samples of ornament) and aperture shapes for representative specimens ordinated against diameter and stratigraphic level. Similarity is generally between smaller stratigraphically lower specimens and larger, higher specimens. This is particularly true with respect to the characters which comprise the first principal component (see Table 1): whorl width ($S$), whorl expansion rate ($W$), diameter of umbilicus ($D$), coarseness of ornament ($LT$, $HT$, $T$), depth of hypnomic sinus ($HS$), bifurcation of striae ($BIF$). The acute venter shown by the two larger specimens is apparently associated with approach of maturity in some reticuloceratids.

For each zone, morphology is shown for two or three ontogenetic stages of a species which is, where possible, representative and average for the fauna, as ascertained from the graphs shown in text-fig. 4. The species illustrated are, in ascending order: level 6—*Homoceratoides prereticulatus*, $H_{2c}$ zone; *Phillipsoceras inconstans*, $R_{1a1}$ zone; *P. alpharhipaeum*, $Nm_{2b2}$ zone; level 7—*Tectiretites posterus*, $Nm_{2b3}$ zone; level 9—*Cancelloceras rurae*, $Nm_{2c2}$ zone; *C. martini*, $G_{1a}$ zone. A sliding scale is used—5 mm scale bars are shown for each sketch.

TEXT-FIG. 6. Size *versus* second principal component score for all analysed species with at least part of ontogeny in morphotype III. Data from same species connected by lines. Data for each of the four stratigraphic levels (6–9) plotted separately; labelling on all axes as for level 9.

Through levels 6 to 8 the ancestral P.C. score at larger sizes is shown by descendants at smaller sizes.





TEXT-FIG. 7. The development of morphotype III, illustrated by sketch profiles (with samples of ornament) and aperture shapes for representative specimens ordinated against diameter and stratigraphic level. Similarity is generally between larger, stratigraphically lower specimens and smaller, higher specimens. This is particularly true with respect to the characters which are important in the second principal component (see Table 1): whorl width (*S*), depth of hyponomic and ocular sinuses (*HS*, *OS*), presence of groove in the ventro-lateral region (*VLG*).

For each level, two ontogenetic stages are shown of a species which is, where possible, representative and average for the fauna, as ascertained from text-fig. 6. Species illustrated are: level 6—*Phillipsoceras inconstans*, $R_{1a1}$ zone; level 7—*Reticuloceras reticulatum*, $R_{1c}$ zone; level 8—*Bilinguites gracile*, $R_{2a}$ zone; level 9—*B. superbilingue*, $R_{2c}$ zone. Scale bars 5 mm are shown for each sketch.
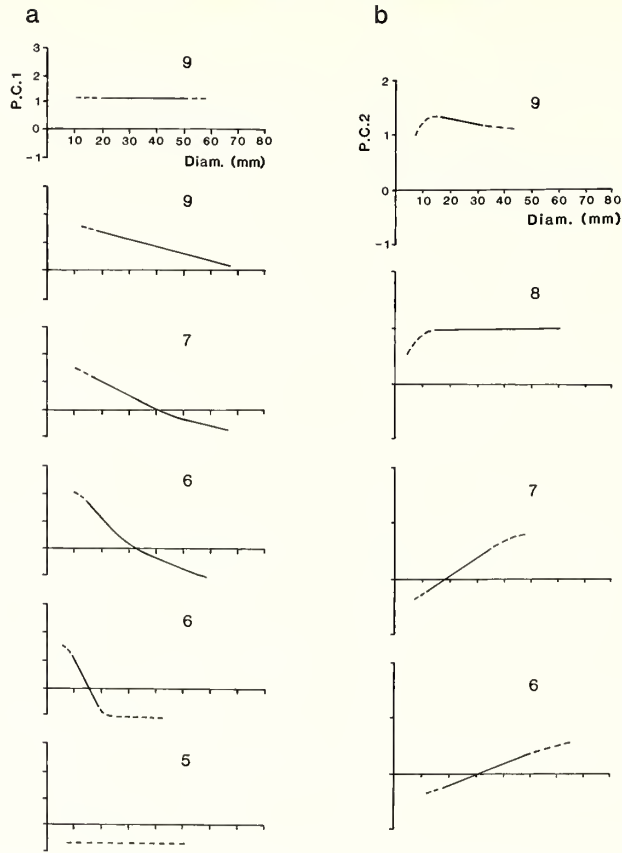
TEXT-FIG. 8. Interpretations of evolutionary trends in ontogenetic trajectories through time. Dashed lines indicate extrapolation beyond the available analysed data. *a*, Morphotype VIII. The ancestor in level 5, in common with other early gastriocerataceans, probably showed ontogenetic transition between morphotypes VII and V (see text-fig. 3). As P.C.1 is used here as an index of the morphotype VIII direction, the level 5 trajectory can be regarded as flat. The innovation of morphotype VIII in level 6 is cenogenetic, involving just the smaller stages, and further development is by decrease in the gradient of the trajectory, suggesting neoteny. Compare with text-fig. 2. *b*, morphotype III. The interpretation of low P.C.2 scores for small stages (< 10 mm) in levels 8 and 9 is based on unanalysed evidence (see text). The trajectories show an evolutionary increase in gradient, suggesting acceleration, though this is constrained by an upper limit to the P.C.2 score.

is *Homoceratoides prereticulatus* from the $H_{2c}$ zone, which is not regarded as ancestral to the reticuloceratids either by Bisat (1933), who derived this species and the reticuloceratids separately from *Homoceras*, nor by Ruzhencev and Bogoslovskaya (1978, p. 59), who placed the genus in a different superfamily, the Thalassocerataceae, and derived the reticuloceratids from *Surenites*. Nevertheless, *Homoceratoides prereticulatus* does show similarities with Russian *Surenites* and *Brevikites*; this suite of taxa is in need of systematic revision. On balance, the $H_{2c}$ zone fauna should not be regarded as an integral part of the documented evolutionary trends. The earliest contribution from the Urals is a species of *Surenites* in $Nm_2b_1$ zone, which can be included with greater confidence.

The derivation of the Gastrioceratidae from the Reticuloceratidae is also debatable. Bisat (1933) postulated an origin for the family in *Homoceras*, but this is not supportable in the light of more recently available information. Ruzhencev and Bogoslovskaya (1978, p. 60) preferred *Surenites*

TEXT-FIG. 9. Decline in gradient of morphotype VIII onto-
genetic trajectories through time. Faunal averages are plot-
ted for each of the zones shown in text-fig. 4. Triangles
North-West European faunas; circles, South Urals faunas.
Open symbols denote faunas which are phylogenetically
distinct from the main morphotype VIII lineage, or are
doubtful.
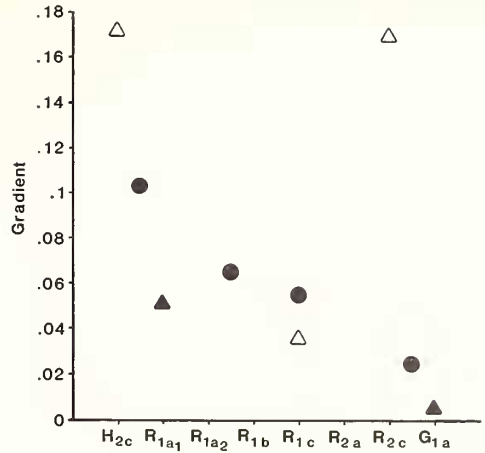


$(Nm_2b_2)$ via *Monitoceras* $(Nm_2c_1)$ as an ancestor, but without any record of the lineage in $Nm_2b_3$ zone. I (Swan 1984, p. 196) have emphasized the close similarity between *Cancelloceras* $(Nm_2c_2)$ of the Gastrioceratidae with *Alurites* $(Nm_2b_{2-3})$ of the Reticuloceratidae. An origin for the Gastrioceratidae amongst the morphotype VIII reticuloceratids of level 7 is most likely, and the validity of the evolutionary comparison is sustained for these groups. Note, however, that this lineage does not include the European specimens of *Bilinguites* from zones $R_{2a}$ and $R_{2c}$, plus *Reticuloceras* in $R_{1c}$, which stray into morphotype VIII. These can be eliminated from further considerations regarding the morphotype VIII lineage.

The other major assumption, the standardization of ontogeny by size, needs careful appraisal. If the size–age relationship and the size at maturity were constant through the Namurian, then the evolutionary trend in morphotype VIII is certainly neotenous, as the size axis of text-figs. 4 and 8a would be directly comparable to the age axis in text-fig. 1. An error in the assumption of constant size at maturity would not directly affect this result, as this is only critical in discerning hypermorphosis and progenesis, and does not affect the gradient of the ontogenetic trajectory (text-fig. 1). An error in the assumption of constant size–age relationship, however, could affect the hypothesis of neoteny. For example, more rapid growth in a descendant (resulting in proportioned gigantism if life-span is retained) would not affect the shape–age curve, so could not be termed neoteny, but would decrease the gradient on a shape–size curve. The distinctions between neoteny and proportioned gigantism on a shape–size curve are the length of the trajectory (proportioned gigantism results in attainment of larger size) and the consequent attainment by proportioned giants of all morphologies present in the ancestor. Thus the descendant gastriocerataceans, for example in level 9, would be derived by proportioned gigantism (rather than neoteny) from their ancestors, for example in level 6, if the complete ontogenies of the former continue beyond the apparent maximum size to cover the morphologic range of the latter. The observed ontogenetic gradients (text-fig. 9) indicate that this would require an increase in maximum size of the descendant over the ancestor by a factor of more than 5. Published and other data suggest that the phyletic size trend involves less than a twofold increase (text-fig. 10a), and this may be overestimated due to the bias imposed by frequent fragmentation of larger specimens in the earlier European faunas. The data are then only compatible with proportioned gigantism if the ontogeny of the 'giants' were shortened by progenesis. This hypothesis can be regarded as less likely than neoteny by the simple application of Occam's razor.

In conclusion, although Gould (1977) argued that the 'restricted model' used here of 'standardiza-tion by size' cannot yield definitive heterochronic results, it is clear that, following a cenogenetic innovation, neoteny is the most parsimonious hypothesis for the evolutionary development of
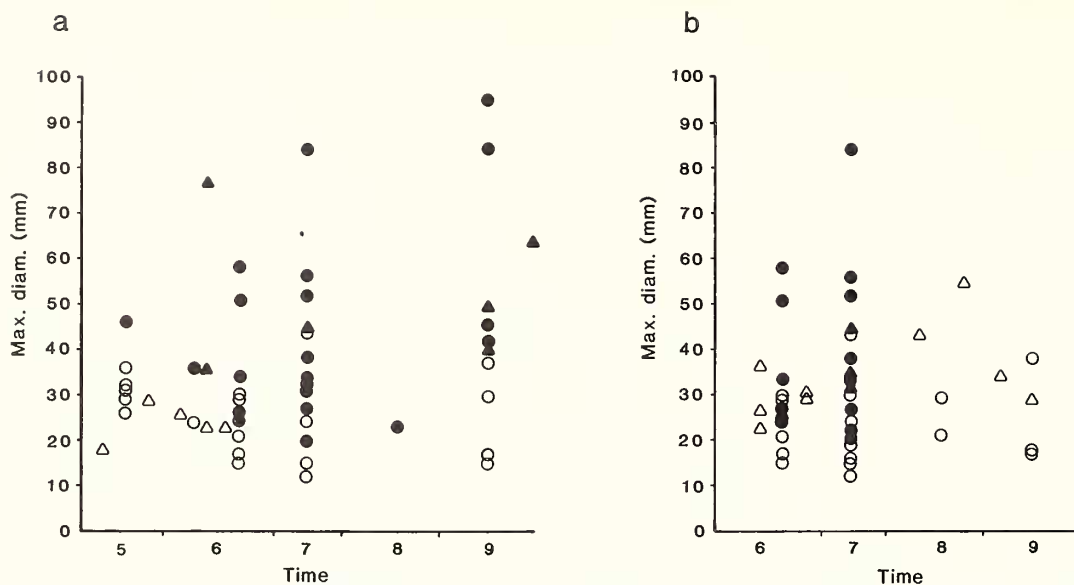
TEXT-FIG. 10. Species size through time for *a*, morphotype VIII, *b*, morphotype III. The maximum recorded diameters for all species allocatable to the respective morphotypes are plotted. Triangles, North-West European species; circles, South Urals species. Solid symbols are used where specimens show some sign of approaching maturity (e.g. loss of ornament, change of aperture shape), open symbols denote specimens without such indication (though this may be due to lack of morphological change at maturity).

Overall, the size trends through time are not sufficient to account for the evolutionary trends as gigantism or dwarfism.

morphotype VIII by the Gastriocerataceae. This combination of modes of evolution is identical to proterogenesis of Schindewolf (1936).

*Morphotype III*

The important trends apparent from the graphical results (text-figs. 6 and 7) and the interpretation (text-fig. 8*b*) are in contrast to those of the previous morphotype. First, the innovation of the morphology is in the larger ontogenetic stages, with positive slopes on ontogenetic trajectories in levels 6 and 7. Secondly, the gradient of the trajectories at smaller sizes is interpreted as becoming steeper higher in the Namurian, though the trajectory levels off at larger sizes. Unfortunately, this second contention requires knowledge of specimens from levels 8 and 9 of smaller sizes than those for which data are available for analysis. However, the interpretation of a low or negative P.C.2 score for early ontogenies in levels 8 and 9 is supported by Bisat (1924, p. 116), who states that the lateral lingua (a distinctive characteristic of morphotype III) are not developed until 5 mm diameter.

The increase in slope of the ontogenies through time is compatible with the hypothesis that heterochronic acceleration has occurred. In this mode, descendants recapitulate ancestral ontogeny, and may transcend it in late ontogeny by simple extrapolation of ontogenetic trends. The negative slope on the trajectory in level 9 (text-fig. 6), if representative, suggests a minor cenogenetic event, but is insufficient to warrant further consideration.

The hypothesis of acceleration for morphotype III is subject to the same constraints as was neoteny for morphotype VIII. First, the assumption of descent needs to be justified, but here this involves fewer uncertainties. There is complete agreement amongst all workers that the progressive accentuation of the morphology of *Bilinguites* (levels 8 and 9) from *Reticuloceras* (level 7) represents

a monophyletic lineage. Indeed, Bisat (1924) described successive species, now allocated to *Bilinguites*, as 'mutations' of *R. reticulatum*. The derivation of this lineage in level 6 is less certain, but is clearly within the reticuloceratids, and the ancestral ontogeny must necessarily have shown a low gradient of morphological change in the direction of the morphotype III vector.

The problem of the standardization by size can be assessed using the same logic as for morphotype VIII. Acceleration would not be a supportable hypothesis if the change of gradient of the shape-age size curve was due to change of rate of growth rather than change in the gradient of the shape-age curve. This would require that descendants grew slower but with the same timing of shape changes, which would result in proportioned dwarfism. The change in size of species necessary to explain the slope changes is approximately a 10-fold decrease. The hypothesis of dwarfism is not supported by data on species size through time (text-fig. 10*b*), which shows little if any trend. Dwarfism is only tenable as an explanation if accompanied by a delay in timing of maturation (hypermorphosis) so that larger sizes were attained. This combination must be deemed less likely than simple acceleration.

## DISCUSSION

Neoteny and acceleration, then, are the most likely processes to have dominated the evolutionary trends of the two ammonoid groups studied. Although few species-to-species lineages are known with confidence, the systematic trends, involving large numbers of species through a substantial period of time, are sufficient indication of the operation of heterochrony. It remains to assess the importance of heterochrony relative to other modes of evolution, and to infer its significance with regard to the organisms and their environment.

### How much heterochrony?

The lack of evolutionary lineages forbids an estimate of the number of actual species-to-species transitions which were affected by heterochrony. The percentage of gastrioceratacean genera affected by the documented heterochronic trends, however, is 60–70 %, and there may be other, more subtle heterochronic events in the residual genera. Other Namurian superfamilies, for example the Prolecanitaceae, Medlicottiaceae, Dimorphocerat.aceae, and Goniatitaceae, do not exhibit extreme ontogenetic changes in external morphology, and evolve comparatively little in the Namurian, so for these groups heterochrony is less likely and would be difficult to detect. Amongst the Neoglyphioceratataceae, however, the derivation of the genus *Eumorphoceras* from the Dinantian *Girtyoceras* closely parallels the origin of *Bilinguites* recorded here, and probably involved the same process. A minimum estimate for Namurian genera affected strongly by heterochrony is 25 % (approximately 20 % neoteny, 5 % acceleration). Interestingly, these genera supply about one-half of the zonal ammonoid species in the USSR and about two-thirds in the USA and North-West Europe. Either heterochrony is important in the rapid evolution necessary for zonal division, or the rapidity enables the mode of evolution to be deciphered.

Within the heterochronic trends, the effect of heterochrony relative to other, less systematic evolutionary modes can be estimated. The first three principal components of variation, in which we know the distribution of specimens of morphotypes VIII and III, comprise 45·8 % of the total variation: 24·4 % in P.C.1; 12·3 % in P.C.2; 9·1 % in P.C.3 (Table 1). For morphotype VIII, removing the cenogenetic effect and the randomizing, non-heterochronic scatter, we can estimate that about half of the P.C.1 and P.C.2 directions of variation are due to neoteny; that is 18 % of the total or about 40 % of the first three principal components. For morphotype III there is less scatter in P.C.s 2 and 3 but more in P.C.1; the estimated percentages are 23 % of the total, 50 % of the first three principal components. The degree of scatter within the morphotypes with respect to the remaining components of variation can be assumed to be similar, so that the latter figures (40 % and 50 %) are realistic estimates for the contribution of heterochrony.

*Why heterochrony?*

In interpreting evolution by heterochrony, mention must first be made of Gould's (1977) attempt to link progenesis with r-type and neoteny with K-type ecological strategies. Progenesis, involving early maturity at the expense of morphological specialization, is plausibly claimed by Gould to be advantageous for rapid turnover of generations in order to exploit ephemeral resources. His contention that neoteny is a good K-strategy is less logical: morphological 'fine-tuning' to a stable environment is not an automatic result of neotenous juvenilization. Hypermorphosis is the more apparent converse of progenesis. Neoteny is clearly only advantageous if the ancestral immature morphology is more successful than the ancestral mature morphology in the particular environmental situation of the mature descendant. The review by Stearns (1976) of the complexity of life history strategies and the problems of assessing competing hypotheses is an adequate critique of such simplistic models, and Alberch *et al.* (1979, p. 314) conceded that much depends on the properties of the specific environment and organism being studied.

Spectacular anisometric ontogenies are well known amongst heteromorph ammonites, and have invited speculation about changes in mode of life, for example by Klinger (1981). Changes in Palaeozoic ammonoid ontogenies are more subtle, but have been analysed by Kullman and Scheuch (1970) and by Kant and Kullman (1978), who consistently detected abrupt changes in allometric growth constants, but did not attempt a functional interpretation. There is no previous literature on Carboniferous ammonoid life history.

Swan and Saunders (1987) presented a detailed analysis of the functional morphology of Namurian ammonoids. Using evidence from hydrostatics, hydrodynamics, apertural morphology, ornament, and facies associations, modes of life were postulated for each of Saunders and Swan's (1984) morphotypes. Results relevant here are as follows: morphotype VIII shows a suite of characteristics (high drag coefficient, low aperture orientation, potentially cryptic ornament, etc.) all compatible with a benthic mode of life; morphotype III (with streamlined shell and strong, high hyponome) was probably nektonic and pelagic; morphotype V, which was adopted by the mature ancestors of the innovators of both morphotypes VIII and III, is interpreted as versatile, nekto-benthic; and morphotype VII, which may have been the immature morphology of the morphotype VIII ancestors, was probably a less sophisticated benthic adaptation. This functional morphological analysis was based on data from ammonoids at various sizes, and the functional interpretations are largely independent of size (the exception being a small component of hydrodynamic behaviour, Chamberlain 1981). Consequently, these results can be used in interpreting not only differences between species but also changes in morphology during ontogeny.

The ontogeny of the immediate ancestor of the morphotype VIII innovator probably included a transition from morphotypes VII to V: this is almost ubiquitous for the early Gastrioceratacceae. This may be interpreted, following Swan and Saunders (1987) as a transition from a benthic adolescence towards greater versatility by improved swimming ability at maturity. The cenogenetic evolution of morphotype VIII did not change this basic scenario: morphotype VIII differs from VII only in ornament. The new distinctive ornamentation may have been cryptic in effect and developed in response to predation of juveniles. The subsequent neotenous advance of this morphology to later ontogeny suggests that benthic conditions became suitable for the entire life history of the individual; the previously advantageous versatility at maturity became redundant. High mobility may not be necessary before maturity where there are strongly localized resources which can be intensively exploited, but in these circumstances mobility is important at maturity for genetic variability in mating and for appropriate siting of eggs (as in caterpillar and imago stages of butterflies). The neotenous progression of morphotype VIII may reflect an improvement in the quality and lateral extent of benthic habitats, so that these habitats could support the entire ontogeny of ammonoids, and allow sufficient lateral migration without the requirement of strong swimming ability.

The ancestor of the morphotype III *Reticuloceras–Bilinguites* lineage would, in common with other early reticuloceratids, have shown an ontogenetic transition from morphotype VIII to V. According to Swan and Saunders' (1987) work, this corresponds to a change from benthic to

nekto-benthic, with improvement in swimming ability. The initial foray into morphotype III occurred in late ontogeny by exaggerated development of a suite of characters: compression, involuteness, smoothness, depth of hyponomic, and ocular sinuses. These characters favour hydrodynamic efficiency, and the evolutionary development of the morphotype indicates further improvement of swimming ability and less dependence on the benthic environment. The subsequent acceleration of these characters in *Bilingnites* had the effect of pushing this morphology into earlier ontogeny. In this way, less of the ontogeny remains suitable for a benthic existence until, in level 8, all but the first 5 mm is well adapted to a nektonic, pelagic lifestyle. It is notable, however, that even in the terminal extreme of this lineage (represented by *B. superbilingue*), the available material showing early ontogeny, though usually poorly preserved, appears to retain vestiges of morphotypes V and VIII. The ontogeny, therefore, is condensed by pure acceleration and not by deletion (Gould 1977, p. 75). It seems that the ancestral morphologies have been regressed into early ontogeny as much as the process of acceleration allowed. In contrast to morphotype VIII, there is a strong trend in this lineage to reduce the dependence on the benthic environment as much as possible.

The evidence here, then, does not support the concept of a profound relationship between ontogeny and phylogeny envisaged by Haeckel (1866) and other nineteenth-century philosophers, or the importance of the cryptogenic juvenile innovations of Schindewolf's proterogenesis; nor does it support Gould's (1977) hypothesis of ecological stragegies. Rather, the heterochronic mode was determined by specific features of the organism's ontogeny and specific aspects of the changing environment. Thus, it appears that if an ammonoid ancestor was successful by being morphologically adapted to exploitation of habitat X in early ontogeny and habitat Y in late ontogeny, then if habitat X disappeared, a peramorphic descendant was 'naturally selected', if habitat X improved, then a descendant was likely to be paedomorphic.

*Namurian environments*

The possibility emerges from the preceding discussion that there is evidence for two contrasting environmental trends in the Namurian. The morphotype VIII development suggests improving benthic conditions through the latter half of the series; morphotype III, in apparent contradiction, may reflect a phase of deteriorating benthic conditions, perhaps due to anoxia. (The possible importance of benthic anoxia in ammonoid evolution was proposed by House 1985.) Saunders and Swan (1984) contended that the changes in morphologic diversity in the Namurian were, in general, synchronous world-wide; the possibility of global environmental changes demands more detailed investigation.

In terms of abundance and rate of neotenous evolution, morphotype VIII is strongest in zones $R_1$ and G (Russian $Nm_2b$, $Nm_2c_2$); in the higher $R_1$ the development is considerably stronger in the carbonate shelf of the South Urals than in the basinal shales of North-West Europe (text-fig. 4). In the intervening zones ($R_{2a,b,c}$, $Nm_2c_1$), however, the morphotype is rare everywhere, represented only by *Bilingnites* derivatives and early gastrioceratids, all the typical morphotype VIII reticuloceratid genera having become extinct. This period coincides with the rise of morphotype III, the maximum rate of acceleration for which was in zones $R_{1c}$ to $R_{2c}$ ($Nm_2b_3$ to $Nm_2c_2$), with greater abundance in North-West Europe. Following the resurgence of morphotype VIII, *Bilingnites* declines in abundance markedly. In the European G zone, *B. superbilingue* occurs occasionally in thin layers within *Cancelloceras*-dominated horizons and declines upwards; in the South Urals, *Bilingnites* is only common in association with the earlier species of *Cancelloceras*, *C. rurae* (Ruzhencev and Bogoslovskaya 1978, pp. 6–26). Investigation of these trends amongst other superfamilies is not without difficulties: as might be expected, morphologies interpreted as strongly pelagic (e.g. *Dimorphoceras, Anthracoceratites*) are unaffected by the inferred benthic changes, and the remaining examples of benthic morphotype VII are difficult to interpret (e.g. *Syngastrioceras*, see Swan and Saunders 1987). The benthic morphotype VI, however, does decline in parallel with VIII.

This evidence, then, is generally compatible with the following sequence of events: 1, development of morphotype VIII during radiation into diverse benthic habitats resulting from eustatic

transgression in late H zone ($Nm_2b_1$); 2, neotenous progression of morphotype VIII in the Gastriocerataceae particularly in shelf carbonate environments of the Urals in $Nm_2b_2$ and $Nm_2b_3$ zones, whilst morphotype III begins to develop by acceleration in reticuloceratids due to deteriorating benthic oxygenation in Europe; 3, poor benthic conditions widespread in $R_2$ zone ($Nm_2c_1$), morphotype III proliferates whilst morphotype VIII survives in few remaining favourable niches; 4, benthic conditions improve in G zone ($Nm_2c_2$), surviving examples of morphotype VIII re-radiate and morphotype III gradually becomes obsolescent. It must be emphasized, though, that the quality of the evidence ensures that this scenario is no more than a tentative hypothesis.

## SUMMARY

A comprehensive body of morphological data for nearly all known Namurian ammonoid species at various sizes and localized in space and time provides a suitable data base for the comparison of ontogenetic and phylogenetic trends. Scores on axes representing principal components of variation give a good estimate of shape, and ontogenetic trajectories can be constructed by ordination against size. Differences between ancestral and descendant ontogenies can then be compared with models of heterochronic results.

Despite the crude estimation of ontogenetic stage by size and the poor resolution of evolutionary lineages, careful appraisal of the data leads to the parsimonious conclusion that the development of two gastrioceratacean morphological radiations was strongly affected by heterochrony. A depressed, evolute, coarsely ornamented morphotype (VIII) evolved by proterogenesis, comprising an initial cenogenetic event followed by neoteny; the compressed, involute, smooth morphotype with deep hyponomic and ocular sinuses (III) apparently developed by acceleration. Evolution by heterochrony is estimated as having affected a minimum of 25 % of Namurian ammonoid genera, which includes the majority of biostratigraphic index species.

Functional morphological analysis of Namurian morphotypes suggests that heterochrony is not in itself an ecological strategy for this group. From ancestral ontogenies involving adaptation to a change in mode of life from benthic to nekto-benthic, neoteny allowed specialization to benthic habitats throughout ontogeny, and acceleration diminished the benthic stage in favour of nektonic ability. For this type of evolution, heterochrony is appropriate in that whole morphology can be transferred to different positions in ontogeny, by single changes in regulatory genes.

Cosmopolitan trends in Namurian ammonoid evolution lead to the suggestion that the development of morphotype VIII occurred in response to improving benthic conditions in zones $R_1$ and $G_1$, whereas the success of morphotype III could be a symptom of widespread reduced benthic oxygenation in $R_2$ zone.

## REFERENCES

ALBERCH, P., GOULD, S. J., OSTER, G. F. and WAKE, D. B. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology*, **5**, 296–317.

BISAT, W. S. 1924. The Carboniferous goniatites of the North of England and their zones. *Proc. Yorks. geol. Soc.* **20**, 40–124.

——1933. The phylogeny of the North of England goniatites. *Proc. Geol. Ass.* **44**, 255–260.

CHAMBERLAIN, J. A. 1981. Hydromechanical design of fossil cephalopods. *In* HOUSE, M. R. and SENIOR, J. R. (eds.). *The Ammonoidea. Syst. Ass. Spec. Vol.* **18**, 289–336. Academic Press, London.

DE BEER, G. R. 1930. *Embryology and evolution*, 116 pp. Clarendon Press, Oxford.

GOULD, S. J. 1968. Ontogeny and the explanation of form: an allometric analysis. *In* MACURDA, D. B. (ed.). Paleobiological aspects of growth and development, a symposium. *Paleont. Soc. Mem.* **2**, 81–98.

—— 1977. *Ontogeny and phylogeny*, 501 pp. Harvard University Press, Cambridge, Massachusetts.

HAECKEL, E. 1866. *Generelle Morphologie der Organismen*, 2 vols., 574 pp., 462 pp. Georg Reimer, Berlin.

HOUSE, M. R. 1985. Correlation of mid-Palaeozoic ammonoid evolutionary events with global sedimentary perturbations. *Nature, Lond.* **313**, 17–22.

HYATT, A. 1889. Genesis of the Arietidae. *Bull. Mus. comp. Zool. Harv.* **16** (3), 1–238.

KANT, R. and KULLMAN, J. 1978. Gehause-Allometrie bei Cephalopoden. *Neues Jb. Geol. Paläont. Abh.* **157**, 98–103.

KENNEDY, W. J. and COBBAN, W. A. 1976. Aspects of ammonite biology, biogeography and biostratigraphy. *Spec. Pap. Palaeont.* **17**, 1–94.

KLINGER, H. C. 1981. Speculations on buoyancy control and ecology in some heteromorph ammonites. *In* HOUSE, M. R. and SENIOR, J. R. (eds.). *The Ammonoidea. Syst. Ass. Spec. Vol.* **18**, 337–335. Academic Press, London.

KULLMAN, J. and SCHEUCH, J. 1970. Wachstums—Anderungen in der Ontogenese Paläozoischer ammonoideen. *Lethaia*, **3**, 397–412.

MCNAMARA, K. J. 1982. Heterochrony and phylogenetic trends. *Paleobiology*, **8**, 130–142.

—— 1986. A guide to the nomenclature of heterochrony. *J. Paleont.* **60**, 4–13.

NEWELL, N. D. 1949. Phyletic size increase, an important trend illustrated by fossil invertebrates. *Evolution*, **3**, 103–124.

RAMSBOTTOM, W. H. C. 1977. Major cycles of transgression and regression (mesothems) in the Namurian. *Proc. Yorks. geol. Soc.* **41**, 261–291.

RUZHENCEV, V. E. and BOGOSLOVSKAYA, M. F. 1978. Namyurski ctap y evolyutsii ammonoidei. Pozdenamyurskiye ammonoidei. *Trudy paleont. Inst.* **167**, 1–336.

SAUNDERS, W. B. 1983. Natural rates of growth and longevity of *Nautilus belauensis. Paleobiology*, **9**, 280–288.

—— RAMSBOTTOM, W. H. C. and MANGER, W. L. 1979. Mesothemic cyclicity in the mid-Carboniferous of the Ozark shelf region? *Geology*, **7**, 293–296.

—— and SWAN, A. R. H. 1984. Morphology and morphologic diversity of mid-Carboniferous (Namurian) ammonoids in time and space. *Paleobiology*, **10**, 195–228.

SCHINDEWOLF, O. H. 1936. *Palaontologie, Entwicklungslehre und Genetik*, 108 pp. Berlin.

STEARNS, S. C. 1976. Life-history tactics: a review of the ideas. *Q. Rev. Biol.* **51** (3), 3–47.

SWAN, A. R. H. 1984. A revision of some Silesian goniatites using cluster analysis. Ph.D. thesis (unpublished), University of Leeds.

—— and SAUNDERS, W. B. 1987. Function and shape in late Paleozoic (mid-Carboniferous) ammonoids. *Paleobiology*, **13**, 297–311.

ANDREW R. H. SWAN

Department of Geology
University College
Singleton Park
Swansea SA2 8PP

Present address:

School of Geological Sciences
Kingston Polytechnic
Penrhyn Road
Kingston upon Thames
Surrey KT1 2EE